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Notes on Nearctic Hepaticae VI

PHYTOGEOGRAPHICAL RELATIONSHIPS OF CRITICAL SPECIES IN MINNESOTA AND ADJACENT AREAS OF THE GREAT LAKES

R. M. Schuster[1]

A number of highly disjunct species of liverworts have recently been reported from the Great Lakes region by the writer in a manual on the Hepaticae of Minnesota, published in 1953. Limitations of space, and orientation of objective then prevented as full a discussion of the implications of some of the distribution patterns as would have been desirable. The present publication is intended to discuss the phytogeographical aspects which were not previously treated in detail. In utilizing the present paper, it may prove helpful to refer to the more generalized and abbreviated discussion of the floristic affinities of the Hepaticae of Minnesota (Schuster, 1958). In that paper are given a series of maps which, in part, supplement the maps included here.

The distribution patterns of the bryophytes have not received the attention that they deserve. This is partly due to the fact

[1] The field work leading to the preparation of this paper was supported in part by two grants from the National Science Foundation (NSF Grants 669, 1369); during a portion of the writing of the paper the writer held a Fellowship from the Guggenheim Foundation. I would like to express my appreciation to Drs. W. D. Billings (Duke University), Warren H. Wagner Jr. and Edward Voss (University of Michigan) for critically reading portions of this paper. In the preparation of the original drafts I was assisted by my wife, Olga M. Schuster, who has also assisted in preparing the final draft for publication.

It should be pointed out that the original draft of this paper was written more than five years ago. The accumulation of additional phytogeographical data has been so rapid that the paper has been revised almost annually, greatly delaying its appearance. Several papers in this series (Nearctic Hepaticae, VIII–XI) have, in the meantime, appeared. The phytogeographical data is as complete as possible, up to, and usually including data published in 1956. I have omitted questionable reports, while localities that could not be accurately pin-pointed are indicated with a question mark on the maps. In a few cases stations are known for some species lying in the Aleutian chain of islands, beyond the margins of the map commonly used. An arrow is used to indicate a station (or stations) lying west of the area given on the map.

that an idea still persists that bryophytes do not show as rigidly defined ranges as the higher plants, and thus approach many algae in their distributional peculiarities, or lack thereof.[2] The rate of evolution of the bryophytes is probably much slower than that of many of the genera and families of the angiosperms, with the consequence that there is a slower, and less marked tendency for disintegration into geographical races or varieties. Such "conservatism" of the Bryophyta is, however, of marked advantage for the student of plant distribution, in that the bryophytes may often serve to show past phytogeographical links which otherwise have nearly been destroyed. An example, if one is needed, is the established connection between the flora of western England and Ireland, with that of the Southern Appalachians, that of the coastal portions of Alaska, and that of eastern Asia. The existing distribution of *Herberta sakuraii* serves to emphasize the floristic features these areas once had in common (Schuster, 1957a). The phytogeographical links thus established probably represent remnants of a former, more widespread range. That such connections remain is perhaps partly the consequence of a high "somatic plasticity," and correlated lower evolutionary potential, of many species of Hepaticae. This is especially the case with species which reproduce largely or exclusively by asexual methods. In such cases the chance for genetic recombination is proportionally infrequent or even lacking.

Linked with the inherent evolutionary "conservatism" of many bryophytes is their small size, and consequent ability to survive in limited niches, or microenvironments. The reduced size, as compared with that of seed plants, allows them to survive in small niches, even if they lack the ability to evolve to meet new environmental conditions. In a similar situation, the angiosperms in most cases must either evolve and adapt, or else die out. As a result, bryophytes, in many cases, perhaps have remained as

[2] An equally significant factor in limiting the use of phytogeographical information derived from the Bryophyta is the difficulty of access to such data, and the relatively limited amount of such data available. The effect of recent collections on our concepts is illustrated, for example, by the ranges here plotted for *Diplophyllum obtusifolium* and *Anastrophyllum saxicola*. The writer has collected, in recent years, all of the material from eastern United States of both of these species, with the exception of only one collection. The recognition of these species as elements in the flora of the eastern United States thus is a very recent matter. Equally recent is our still very partial knowledge of the American range of *Scapania scandica*, which is not listed for the western hemisphere in the recent (1938) list of Buch, Evans & Verdoorn, and still listed as only known from Greenland in Frye & Clark (1946, in 1937–47).

relicts in sites where almost all disjunct angiosperms have disappeared and their study, therefore, is pertinent to the whole problem of the evolution of our present flora.

Within the more restricted framework of the phytogeographical affinities of the Great Lakes region, the pertinence of phytogeographical data, derived from bryophytes, has been shown in the pioneer paper of Steere (1937). He pointed out that the same phenomena of disjunction existed among the Great Lakes bryophytes as had been demonstrated by Fernald (1925, 1935) for the tracheophytes. In Steere's paper, the disjunct Bryophyta were treated as members of four floristic elements, as follows:

(1) Arctic species which reach their southernmost point in the Lake Superior region. *Asterella ludwigii* (Fig. 7) is cited as an example.

(2) Almost strictly Cordilleran species, "usually characteristic of high altitudes." *Jungermannia schiffneri* is cited as an example, and a map of its then-known distribution is given (Steere, Fig. 4).

(3) Pacific coast species, usually characteristic of lower altitudes. *Frullania bolanderi* is cited as an example, and its distribution given (Steere, Fig. 5; see Fig. 12).

(4) Cordilleran species, also found (at lower elevations) in the "Driftless Area" of Wisconsin, Iowa, Minnesota and Illinois. An example is cited, *Asterella saccata* (see Fig. 14).

To these distributional types the present writer would add, for the purposes of this discussion, several others:

(5) Arctic species, occurring in the "Driftless Area," but evidently not in the Lake Superior Region. *Athalamia hyalina* (Fig. 15) and *Mannia sibirica* (Fig. 16) have distribution patterns of this type.

(6) Arctic species, occurring southward to the Lake Superior Region, and also in the "Driftless Area." *Mannia pilosa* (Fig. 16) has a distribution pattern of this type.

(7) Appalachian species, with a scattered range into the Ozarks, in some cases to the "Driftless Area" and northward also to the Lake Superior region. *Mannia rupestris* and *Diplophyllum apiculatum* are examples (Figs. 17, 18).

The total effect of the introduction of these additional more or less clearly disjunct vegetational elements serves to attribute to the Great Lakes Area (including the nearby "Driftless Area"), and specifically the region peripheral to Lake Superior, an extremely synthetic and diversified flora, considering that the entire region appears to have been glaciated. In the following discussion, examples of each of the vegetational elements are treated,

followed by a discussion in which these discordant distribution patterns will be briefly analyzed.[3]

(1) ARCTIC SPECIES, REACHING THEIR SOUTHERNMOST RANGE IN THE LAKE SUPERIOR REGIONS (Figs. 1–8)

In general, the species with this type of distribution occur southward (at high elevations) to New England, and (at much higher elevations) southward to varying degrees in the Cordilleran chain. Exceptions are specifically noted.

ODONTOSCHISMA MACOUNII (Aust.) Underw. (Fig. 1). This species, of

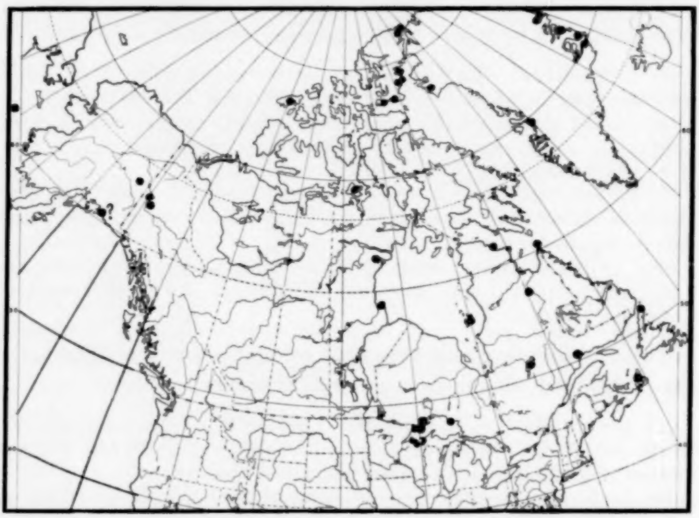

Fig. 1. North American range of *Odontoschisma macounii.*

arctic and alpine distribution in Europe and North America, occurs in a transcontinental belt, lying largely between 55°–82°21′ Lat. N. Eastward it occurs to the south only on Cape Breton I., and on islands in Lake Mistassini; westward it occurs to St. Matthew I. south of Bering Strait. In the United States, it is found only in a restricted area along the North Shore of Lake Superior from Minnesota to Ontario (type), and in Wisconsin and Michigan along the southern shore of Lake Superior. The range is somewhat restricted by the weakly "calciphilous" nature of the species.

[3] Subsequent to the completion of the text and maps, the important paper by Buch & Tuomikoski (1955) on the Hepaticae of Newfoundland, has come to hand. Several of the species treated herein are there extended to Newfoundland.

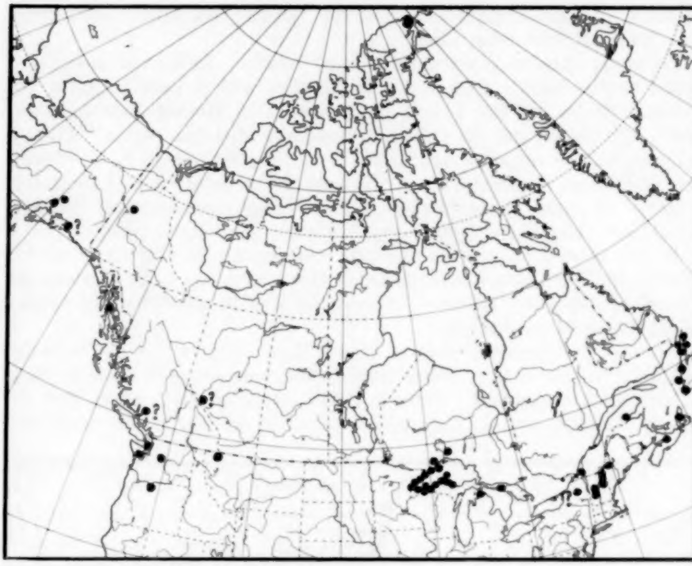

Fig. 2. North American range of *Lophozia (Leiocolea) gillmani.*

Lophozia gillmani (Aust.) Schuster (Fig. 2). A relatively widespread arctic-alpine species more strongly restricted than the last by pronounced Ca requirements. Found in isolated sites, from northeastern Ellesmere I. (*Schuster, 1955*) south to Quebec, Nova Scotia, Vermont and New Hampshire (to the south at medium and high elevations), as well as in the west from the Yukon to the south coast of Alaska, to northern Oregon and Montana. Abundant in the Great Lakes area from Manitoulin I. in Lake Huron to Lake Superior.

Scapania microphylla Wstf. (= *S. buchii* Müller) An arctic-alpine species known from northern Europe, westward to Iceland, reported from one station in Maine, and from Prince Edward I.; recently reported from the north shore of Lake Superior, Lake Region between Minnesota and Ontario, and from Isle Royale, Michigan (Schuster, 1953). An unpublished report extends the species to Wisconsin. This systematically difficult species probably will prove transcontinental when more fully understood.

Lophozia (*Orthocaulis*) quadriloba (Ldb.) Evs. (Fig. 3). Usually considered a high arctic species, with the range in North America almost totally north of the Arctic Circle, north to 83°6′ N. in Greenland and 82°32′ N. in Ellesmere I., only two reports from the high mountains of the Canadian Rockies lying far to the south. Recurring, totally as a

disjunct, at Copper Harbor, and at the "Devil's Washtub," Keweenaw Co., Michigan (Schuster, 1953).

Lophozia (*Leiocolea*) schultzii (Nees) Schiffn. In Europe essentially arctic in distribution, but in North America with a peculiar range involving Alaska and the Yukon, the west coast of Hudson Bay (*Schuster, 1955*), the Gaspé, and the Lake Superior-Lake Michigan region. The totally anomalous report of the species from Bergen Swamp, N. Y. (Schuster, 1949) must be interpreted in the light of the occurrence at the latter locality of many western and Great Lakes species, i.e., *Solidago houghtonii*; the species there is certainly a late Pleistocene relict.

In the absence of reports from the eastern Arctic, the range of this species, in North America, approaches the next group to be treated, the Cordilleran species. However, it must be kept in mind that the species is an obligatory calciphyte.

Scapania scandica (Arnell et Buch) Macv. (Fig. 4). Until recently, the only reports of this species from North America were those of Buch (1928) from Greenland. Persson (1946) reported the species first for North America proper, the species occurring in four widely separated

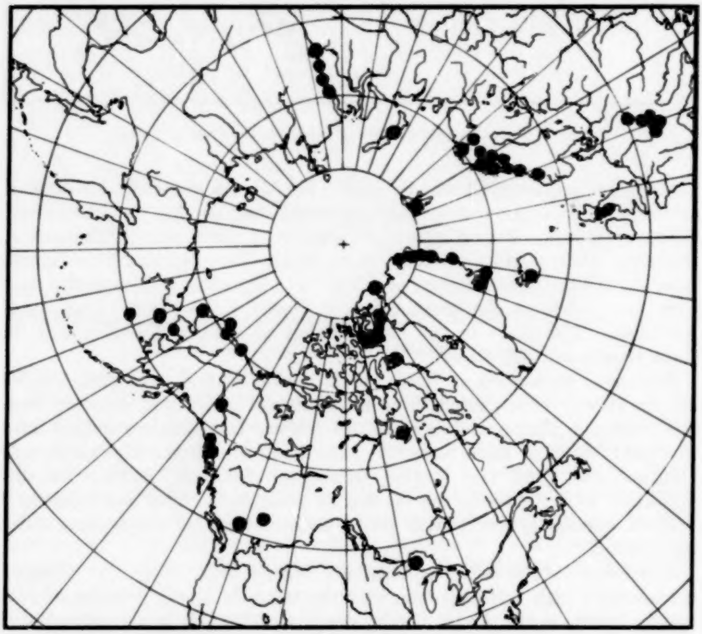

Fig. 3. World range of *Lophozia (Orthocaulis) quadriloba*. Not all stations could be indicated in cases where individual stations are situated less than 100 miles apart.

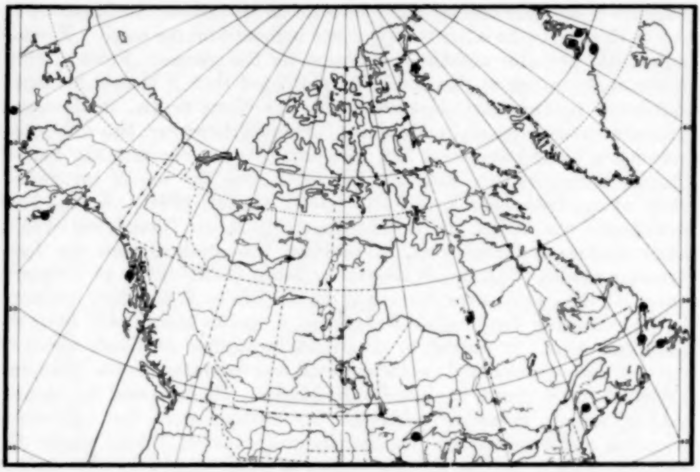

Fig. 4. North American range of *Scapania scandica*.

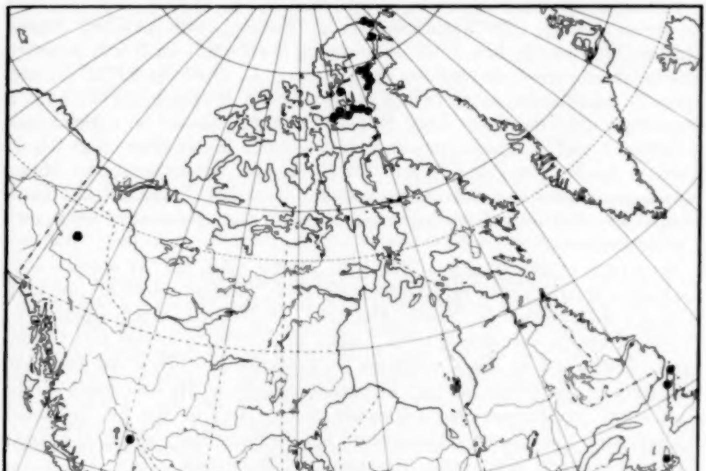

Fig. 5. North American range of *Scapania gymnostomophila* (including *S. incurva*); the British Columbia report uncertain.

localities from Sitka on the southern coast to Kodiak, to St. Matthew I., and to Unalaska (the latter station is not indicated on the map). Persson indicated a probable oceanic distribution for the species. From a study of the entire range of the species I postulated that it should be found southward to Labrador, Newfoundland and Nova Scotia, in the same general areas as *Diplophyllum albicans*. Shortly thereafter, two collections were made by the writer on Mt. Katahdin, Maine: one near the foot of Hamlin Ridge, at only 2800 ft.; the other near the top of the Saddle Slide, at *ca.* 4500–5000 ft. (*Schuster 32910, 32994a*, 1954). A year later the species was found in Newfoundland (Buch & Tuomikoski, 1955). Later during the same year, a specimen was studied from the Lake Superior region, Oak I., Wisconsin (*Cheney 6033*, 1896, as *Scapania curta*; NYBG) which exhibited many similarities to *S. scandica*, but some to the extremely closely allied *S. helvetica*, a species known only from the European Alps. It proved to be almost impossible to decide which of the two taxa was involved, so the material was submitted to the European specialist on the genus, the late Dr. K. Müller. He expressed the opinion that it was *S. scandica*. Although the occurrence of the high-arctic *Scapania spitzbergensis* on Mt. Katahdin (Schuster, 1951a) makes the occurrence there of *S. scandica* a matter of little surprise, the occurrence of *S. scandica* in the Great Lakes region is remarkable.

Scapania gymnostomophila (Kaal.) Kaal. (Fig. 5) (incl. *Diplophyllum incurvum* Kaal.). An arctic species in Europe, with isolated Alpine stations, and one or two in the intervening lowlands. In North America known from numerous stations on Ellesmere I., north to 82°32′ N. and recently established as occurring in the Yukon (Persson, 1952), with a somewhat dubious report from British Columbia (based on a Brinkman collection) and a dubious report from northern Idaho (Frye and Clark, 1946). Again found from Cape Breton I. and Nova Scotia to Maine and Vermont, and in a rather large number of stations in the Lake Superior area. The distribution strongly restricted by the presumably obligatory Ca requirement.

Scapania cuspiduligera (Nees) K. Müller (Fig. 6). A species with as rigid a restriction to calcareous rocks as *S. gymnostomophila*, but with a wider distribution in North America. In Europe, arctic-alpine. In North America widespread from Alaska to Ellesmere Island and Greenland, southward in the Cordilleras to Colorado and New Mexico, and probably to California (at high elevations only!); in the east south to the east shore of Hudson Bay (Schuster, 1951), and to the St. Lawrence Valley and the Gaspé. Recurring, not infrequently, along the Lake Superior shore in Minnesota, Michigan and Wisconsin.

I have also seen a single collection, of typical material, from the alpine portions of Japan (*Inoue*).

Asterella ludwigii (Schwägr.) Underw. (Fig. 7). Also a "calciphile" and consequently of restricted range. With the exception of a doubtful report from Alaska, restricted to the Cordilleran region of the west, (where frequent at high elevations), and recurring along both the east

Fig. 6. North American range of *Scapania cuspiduligera*. The report of this species from western New York (*fide* W. C. Steere), cited in Schuster (1949) is regarded as questionable.

and west coasts of Greenland, in Baffin I., and at Ungava Bay; a doubtful report from the Gaspé. Known from four stations in the Lake Superior region (Ontario, Minnesota and Michigan). The rapidly increasing knowledge regarding the distribution of this species is clear if the map here given is compared with that in Steere (1937, Fig. 2). It is also illuminating to compare the distribution given for the species by Steere (1937) and by Frye and Clark (1937, in 1937–47). The latter, due to an inadvertent confusion of both the distribution data and the illustrations of the two species (see Schuster, 1953) gave the impression that *A. ludwigii* was a common lowland plant in eastern North America. They "extended" the range south to Missouri and Nebraska, and were followed in this by Whittlake (1954), who was able to "extend" the range of this species even as far south as Arkansas. All these reports are certainly erroneous, and must refer to *A. tenella*, the common lowland species.

ANTHELIA JURATZKANA (Limpr.) Trev. (Fig. 8). A non-calciphile, of

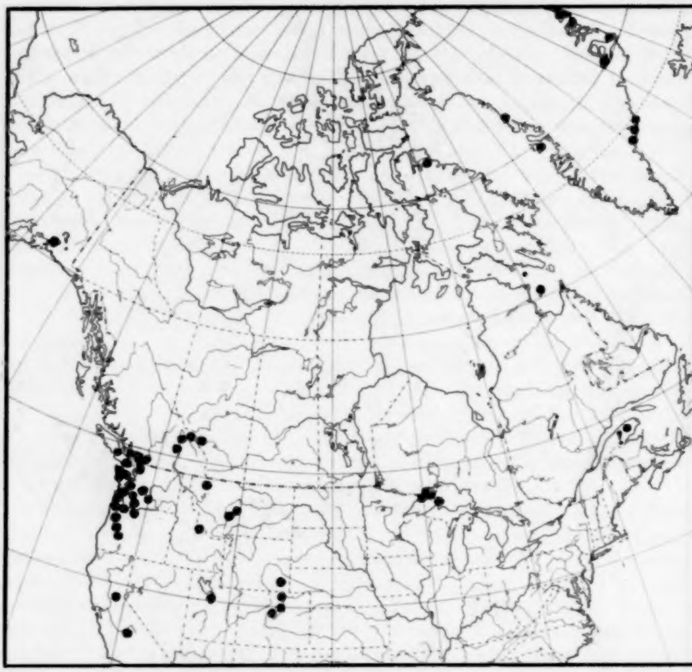

Fig. 7. North American range of *Asterella ludwigii*. The report from the Gaspé uncertain; all of the reports of this species from eastern United States in Frye & Clark (1937) are erroneous.

arctic-alpine distribution, known from the southern coast of Alaska to the Alberta-British Columbia boundary region, south to Wash ngton, and California (locality uncertain), and in the east from Greenland and northernmost Ellesmere I., south to the east coast of Hudson Bay. With a somewhat isolated occurrence on the summit of Mt. Katahdin, Maine (Schuster, 1949), and in the White Mountains of New Hampshire. Totally disjunct at Pictured Rocks, Michigan, on the Lake Superior shore.

Cephalozia leucantha Spruce. A low-grade arctic and subarctic species, apparently lacking in Greenland and Ellesmere I., but with a widespread distribution in the southern portion of the Tundra, and the ecotone between Tundra and Taiga in Quebec, Labrador, and Newfoundland. In addition, a single report from Mt. Marcy, New York (Schuster, 1953), and one from Minnesota (Schuster, 1953). In the west apparently frequent from Alaska, as far west as Agattu I., southward to British Columbia and Washington.

Anastrophyllum saxicola (Schrad.) Schuster (Fig. 9). A rare arctic-alpine species, first reported from the United States from Pigeon Point, Minnesota (Schuster, 1953) but found recently on Mt. Katahdin, Maine (Schuster, August, 1954). The species occurs scattered from Alaska (as far west as Attu I.; station not on map) and the Yukon, and doubtfully to British Columbia, to east Greenland, Baffin I. (Stephani; a recent collection studied from Pangnirtung, *Wynne-Edwards*), Quebec, and the shore of James Bay in Ontario. The species is an oxylophyte.

Very recently a wholly disjunct station of *A. saxicola* has been discovered by the author on Roan Mt., both in Tennessee and North Carolina.

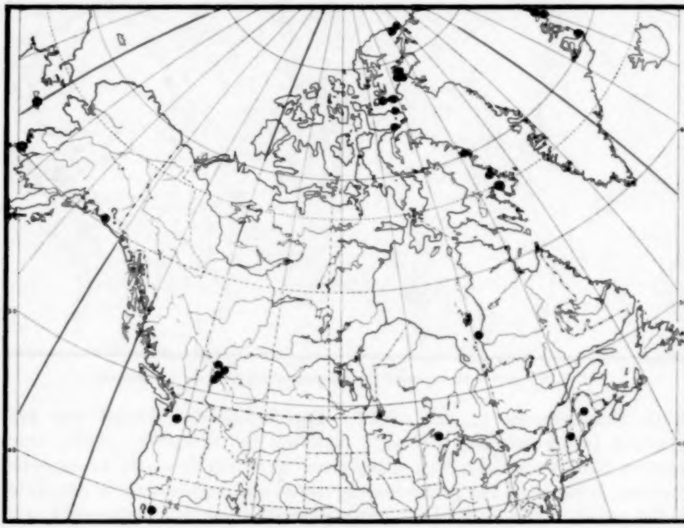

Fig. 8. North American range of *Anthelia juratzkana*.

The occurrence of this arctic-alpine species in the Southern Appalachians, although at first very surprising, is not without parallel. *Sedum rosea*, with the bulk of its range equally in the treeless regions from Labrador to Greenland, occurs as a disjunct on Roan Mt.

Odontoschisma elongatum (Ldb.) Evs. An essentially arctic-alpine species, rare in the Taiga. Widespread in Alaska; recurring eastward on the Greenland coast, the coast of Hudson Bay (Schuster, 1951), southward to the high mountains of Maine and New Hampshire. Recurring as a disjunct, in the Lake Superior area, near Thunder Bay, Ontario, and at Deer Lake, west of Munising, Michigan (Schuster, 1953). Strongly oxylophytic.

Cephaloziella spinigera (Lindb.) comb. n. (based on *Cephalozia spinigera* Lindberg, Musci scand. 4, 1879; *C. subdentata* Wstf., Krypt. Fl.

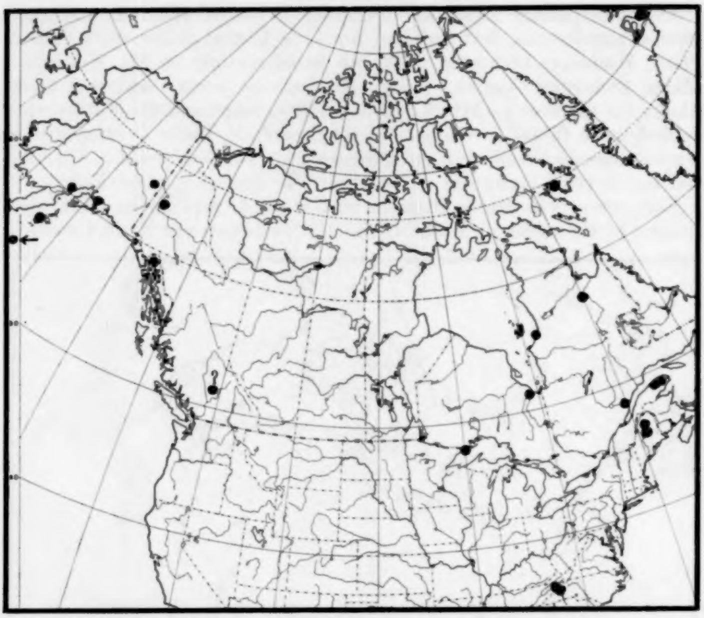

Fig. 9. North American range of *Anastrophyllum* (*Eurylobus*) *saxicola*.

Mark Brandenburg 1: 234, 1902). This helophytic species was first reported from continental North America by Schuster (1949), from western New York—the least likely place in which it would be expected to occur, because of the pronouncedly arctic and high subarctic character of the plant. The bulk of its range extends from St. Lawrence I. and continental Alaska to northern Quebec and Greenland. Collected several times in the high mountains of New England by the writer (Mt. Monadnock and Zealand, N.H.; Mt. Katahdin, Maine), and recently from northeastern Minnesota (Schuster, 1953). The plant is also present in a collection of *Microlepidozia setacea* made in a bog near Burt Lake, Michigan (*Patterson*). This species will probably prove transcontinental in peat bogs and on peat-covered ledges, with the bulk of its distribution in the Arctic.

Scapania degenii Schiffn., ex K. Müll. (Fig. 10) and *Scapania hyperborea*. These closely allied species (Schuster, 1953) are treated as a unit here because of the lack of agreement as to whether the Great Lakes p'ants are to be regarded as *S. hyperborea* or *S. degenii*. Because of their peculiarities, the Lake Superior plants have been regarded as a variety (var. *dubia*) of *S. degenii* (Schuster, 1953). *S. hyperborea* s. str. is frequent, apparently, on the Greenland coast, and occurs on the eastern shore of

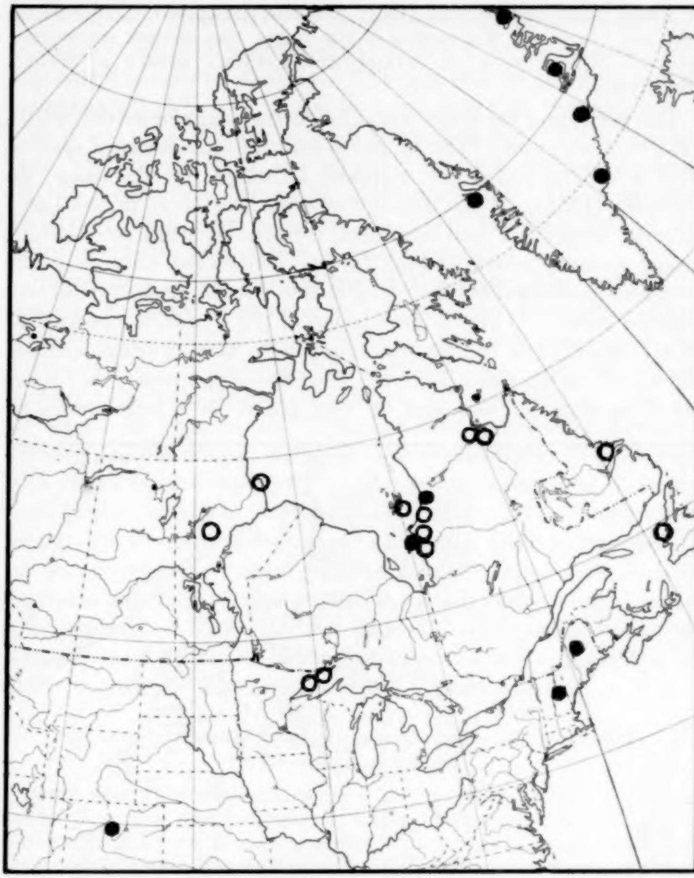

Fig. 10. North American ranges of *Scapania degenii*, including var. *dubia* (rings) and *S. hyperborea* (dots).

Hudson Bay (Lepage, 1953); it was earlier reported by Evans from Maine and New Hampshire, where it is limited to the alpine peaks of the higher mountains. The closely allied *S. degenii* occurs in northernmost Quebec, the Belcher Islands in Hudson Bay, the east coast of Hudson Bay, and near Churchill on the west coast of Hudson Bay, and then recurrs again on the north shore of Lake Superior in Minnesota (Schuster 1951, 1953); a specimen has recently been seen from the coast of Labrador. It was reported from North America only recently, almost simultaneously

by Arnell (1950) and Schuster (1951), and does not appear in the work of Frye and Clark. In the opinion of the writer, two distinct species are involved, *S. hyperborea*, an oxylophyte; *S. degenii*, usually a "weak" calciphyte.

The preceding examples could be further supplemented, without too much point. The ranges of an additional series of species with a similar range are mapped, although not discussed, in Schuster (1958). They demonstrate the existence, in the Lake Superior area, of a well-developed element of arctic and arctic-alpine species, which extend further southward only in some instances (and then at high elevations in the mountains, in all but isolated cases). This, in the opinion of the writer, is clearly due to a microclimatic tundra zone, forming a narrow fringe around the coldest of the Great Lakes. The preceding species, therefore, are to be regarded as a sort of "rear guard" of a larger series of

Fig. 11. North American range of *Jungermannia polaris* (open areas and rings) and of the presumed synonym, *J. schiffneri* (dots).

arctic species, at one time presumed to have characterized much of the raw, recently uncovered soil and rock, at the margin of the receding Pleistocene icesheet. The fact that of these 15 species (haphazardly selected), 8 are to be classified as "calciphiles" is clearly not contradictory to such an explanation. These species, then, are simply relicts, left behind during the northward march of the vegetation after the last glaciation. Their survival locally, in such large numbers, is clearly partially due to the influence of the cold waters of Lake Superior.

Subsequent to the completion of this paper, the writer had occasion to spend a summer in northeastern Ellesmere Island some 40 miles south of the northern tip and 80 miles south of the northern tip of Greenland (the northernmost land area in the world), collecting between Latitudes 82° 24′ and 82° 32′ N. Of these 15 species six (*Odontoschisma macounii, Lophozia gillmani, L. quadriloba, Scapania gymnostomophila, S. cuspiduligera, Anthelia juratzkana*) were found in this area; all of these are "calciphiles" or at least strongly Ca-tolerant. Of the many other largely arctic-alpine species reported for the Lake Superior area, several others were found, among them: *Cephaloziella arctica, Lophozia kunzeana, L. heterocolpa, Lophozia latifolia* and *Cryptocolea imbricata*. The latter two species, only recently described, very rare and restricted in the Lake Superior area, proved to be quite frequent on the north shore of Ellesmere I.!

(2) CORDILLERAN SPECIES OCCURRING AS DISJUNCTS IN THE LAKE SUPERIOR REGION

Steere cites *Jungermannia schiffneri* Loitlesb. (Fig. 11) as an example and gives a map which appears to support this viewpoint. However, this species has recently been reported from Quebec (Lepage, 1945) and is doubtfully known from Ellesmere I., while dubious material is reported as this species from western Pennsylvania. It is probable that a sporadically distributed, widespread arctic-alpine taxon is involved, rather than a *bona-fide* Cordilleran species. The rarity of the species makes it unwise to generalize as to its floristic affinities.[4]

[4] A further complicating factor in interpreting the range of *Jungermannia schiffneri* is the status of the plant known as *J. polaris*. This last was described (as *J. pumila* var. *polaris*) from Spitzbergen material, distributed by Berggren, No. 176, in the Musci Spitzberg., in 1868. Two years later it was raised to a distinct species by Lindberg, and reported from Greenland. Bryhn (1906–1907) reported numerous stations of it from Ellesmere Is. Indeed, judging from the number of stations, this was, on the Second Thule Expedition, the most frequently collected member of the Jungermanniaceae. *J. polaris* was, however, placed as a synonym of the dioecious *Jungermannia atrovirens* by both Stephani and Müller. (*Con't. p. 224.*)

Perhaps no other good case of a species of Hepaticae with a restriction to the Cordilleran area, and an extension to the Lake Superior area is known. This, it should be emphasized, is most easily explained because of the essential lack of a Cordilleran series of species among the Hepaticae. With the greater age of the species, there has been, in virtually no case, divergent evolution of the widespread northern species with an east-west distribution in North America. If maps 1–11 are studied (of the arctic-alpine species), it will be seen that occasional species "approach" the Cordilleran-Great Lakes-St. Lawrence Valley pattern so often emphasized by Fernald. This is the case with *Lophozia gillmani* (Fig. 2) and also *Lophozia schultzii*. These species, however, are obligatory calciphiles, and the disjunction in distribution may be due largely to a disjunction of suitable habitats. As a consequence, the writer cannot at present recognize a Cordilleran element in the hepatic flora of the Lake Superior shore.

The absence of such a Cordilleran element is accompanied by another phenomenon: the frequent Cordilleran extension southward, at high elevations of species I would regard as arctic-alpine in nature. *Scapania cuspiduligera* (Fig. 6), *Asterella ludwigii* (Fig. 7) and *Scapania hyperborea* (Fig. 10) all show such a southward range in the Cordilleras. Any real east-west disjunction appears to be between an oceanic, Pacific element, restricted largely to the Coastal Ranges, and an Appalachian element. Among such examples may be cited *Bazzania denudata* and *Herberta sakuraii* (synonyms are *H. hutchinsiae* and *H. tenuis*; see Schuster, 1957a). East-west disjunction, in the Hepaticae, thus appears to be a phenomenon going back to the early Cretaceous, when the last great submergence of the North American continent took place. This explanation, if tenable, would go far to explain the restriction of a high incidence of "endemics" to the area peripheral to the mid-Cretaceous, Mesocordilleran geanticlinal of the westernmost portion of the continent, and to the Appalachian region to the east. This interpretation would involve, therefore, a pre-Tertiary and at least late Mesozoic origin of some extant species of Hepaticae.

In 1955 I found that the only frequent member of the Jungermanniaceae found on the northeastern coast of Ellesmere I. was the paroecious plant identical in all important respects with *Jungermannia schiffneri*. Subsequently, the collection of Berggren from Spitzbergen, described as *J. pumila* var. *polaris*, alluded to above, was examined. This collection must be considered as the type of var. *polaris*, although it is much less clear that it can serve as the type of the species *polaris*. Careful examination has revealed several pertinent features previously overlooked: (a) the plants are paroecious; (b) the capsules have the median epidermal cells of the valves with 2–4 strong, nodular thickenings on each face of alternating longitudinal walls while those longitudinal walls that alternate with the aforementioned walls lack thickenings or bear 1, rarely 2 thickenings. The cells average 13–15 μ wide. The paroecious inflorescence, as well as capsule-wall anatomy are clearly characteristic of *J. schiffneri*, not of *J. atrovirens* suggesting that *J. polaris* is identical with the later described *J. schiffneri*! Certainly the northern Ellesmere material that I collected in abundance in 1955 is an exact match for the type of var. *polaris*. As a consequence, *J. polaris* (= *J. schiffneri*) now acquires a high arctic range, with isolated stations in the Cordilleras and the Great Lakes region, southward in the east to the montane portions of Quebec (Fig. 11). The species thus clearly acquires a range similar to the arctic and arctic-alpine species previously considered.

Among such species, with a possible origin before the middle Cretaceous are the two following species, both of which are widespread at lower elevations on the Pacific Coast. These species are today found both east and west of the mid-Cretaceous Rocky Mountain geosynclinal, in which the great Cretaceous sea existed.

(3) PACIFIC COAST LOWLAND SPECIES RECURRING IN THE GREAT LAKES AREA

A disjunction of this type is, at first glance, extremely surprising. The classical case is that of *Frullania bolanderi* Aust. (Fig. 12), previously cited by Steere (1937). The considerable expansion in known range in recent years is evident on comparing the map in Steere (Fig. 5) with Fig. 12.

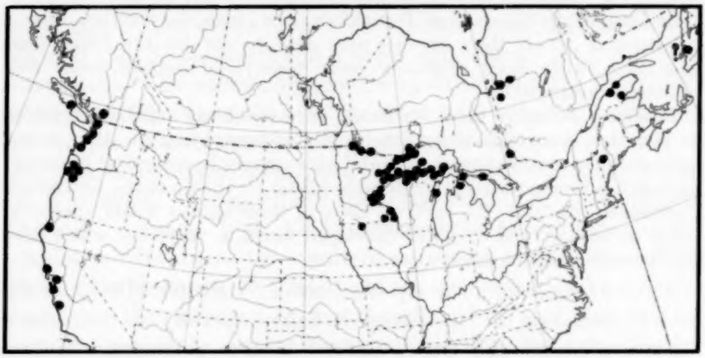

Fig. 12. North American range of *Frullania bolanderi*; the species is otherwise known only from the Pacific Coast of northern Asia.

F. bolanderi was described from near San Francisco, California. It extends from there northward to southern British Columbia, apparently always restricted to relatively low elevations. It then recurs in a disjunct area radiating out from the Great Lakes to the James Bay area, and to the Gaspé, with a single report from Maine. It is reputed to occur eastward to Newfoundland. The explanation of this distribution pattern is particularly difficult in view of the fact that *F. bolanderi* is almost exclusively corticolous, with rare (and probably never permanent) populations on rocks. It is furthermore "critical" in that it is clearly a non-arctic species, which could not have survived in treeless areas, by any stretch of the imagination; it is not known today from any area in immediate proximity to the Tundra. As a consequence, the statement by Abbe (in Butters & Abbe, 1953, p. 69) is of interest. Abbe suggests that the flora of the North Shore of Lake Superior (and specifically that of Cook Co., Minnesota) was not replenished, in late-glacial or post-glacial time from a "pool of 'Cordilleran' or 'arctic' rarities in the Driftless

Area." If this statement by Abbe is accepted as true, the existing range of *Frullania bolanderi* becomes incomprehensible. The simplest explanation for its existing distribution in western North America involves its migration into the Lake Superior area from a Pleistocene "refugium" in the Driftless Area. The suggestively similar case of *Mertensia paniculata* (Ait.) G. Don,[5] known from the periphery of the Driftless Area (n.e. Iowa), the western Great Lakes area, north to James Bay, Quebec; then again in the far West from Montana and Idaho to Washington, is equally impossible of a simple explanation, if Abbe's hypothesis of preglacial migration is uniformly applied. The *Mertensia*, like the *Frullania*, is a plant of forested areas, and not of the tundra. As a consequence, the suggestion that these species migrated into the Great Lakes area at the heels, so to speak, of the retreating glaciers, from a far western "home" is difficult to visualize. More probable, in such cases, is the assumption of "persistence," in the classical Fernaldian sense, with the Driftless Area a refugium in which these species were able to survive the Pleistocene glaciation (while their originally more widespread eastern range was otherwise destroyed).

Frullania bolanderi (and *Mertensia paniculata*) are significant species to consider, from the viewpoint of phytogeography, since they could scarcely have survived in the Great Lakes on any hypothetical nunatak, such as has been postulated by Fernald (1935) for the tip of the Keweenaw Peninsula. At least, the survival there of these species would appear to hinge on the survival of a well-developed forest, a viewpoint which does not deserve serious consideration.

In this connection, the repeated belief by Hultén (1937), in the lack of glaciation on "the islands in Lake Superior," or in nunatak "districts about the Great Lakes" is also pertinent. Hultén (loc. cit., Plate 43) shows such an "isolated" refugium in the Nipigon region of Ontario, north of the North Shore of Lake Superior. As has been repeatedly demonstrated by the geologists (see review in Butters & Abbe, 1953), no such ice-free refugia can be demonstrated. Indeed, the opposite is fairly well-established: all of these areas were glaciated during the Pleistocene. As a consequence of such evidence, the "persistence" theory, so vigorously propounded by Fernald (1925, 1935) has recently received almost no support. In any re-evaluation of the "persistence" theory, however, the evidence from such species as *Frullania bolanderi* must also be considered.

At the time Steere (1937) mapped the range of this species, it was known in the east only from obviously glaciated areas.[6]

[5] The distribution of the various Tracheophyta cited largely derived from the Eighth Edition of Gray's Manual.

[6] Steere (1937) however assigns the eastern stations of the species to "the unglaciated part

Steere postulated that the distribution of the species was broken up into three "remote and isolated 'islands': (1) throughout the Pacific coast area . . . (2) around the southwest end of Lake Superior, and (3) in the unglaciated part of the Gaspé Peninsula of Quebec, with an extension into Maine. . . . This anomalous geographical distribution gains still more significance because of resemblance to that of many of the vascular plants reported from the Keweenaw Peninsula by Fernald." The distribution of these vascular plants, of course, moved Fernald to postulate the occurrence of a nunatak area at the head of the Keweenaw Peninsula (Fernald, 1935), which was believed to have served as a refugium during the late Pleistocene glaciation. Extensive collecting by the writer (1946–1950) in the Great Lakes area soon showed that *F. bolanderi* had a much wider range than had been suspected. The species occurred westward along the Minnesota border to Oak Island, Lake of the Woods; it occurred southward to the presumably partially unglaciated southeastern corner of Minnesota (Schuster, 1953), and it was also found at many points in Wisconsin, Michigan, and into Manitoulin I., Lake Huron, Ontario. Lepage (1945, 1953) extended the known range of the species northward to the southern corner of James Bay. With these extensions, there was a virtual confluence of two of the "islands" that Steere had postulated. More significantly, the known range of the species was extended southward into the edge of the "Driftless Area," an area about which there is no question as to the absence of Pleistocene glaciation. Furthermore, there is clear evidence of the existence, in the Driftless Area, of a well-developed forest, during the Pleistocene (i.e., from the "boreal" rather than arctic nature of the moss flora of the interglacial periods).

These facts prompt the writer to suggest that the eastern portion of the range of this species has radiated outward from the "Driftless Area." The latter, as a consequence, emerges as a possible refugium, postulated as long ago as 1925 by Fernald, who at the time was unable to adduce any concrete evidence in favor of such a viewpoint. In fact, Fernald (1935) fails to mention this earlier hypothesis.

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of the Gaspé Peninsula of Quebec, with an extension into Maine." Recent evidence suggests no such unglaciated area exists.

A final matter of interest is the clear demonstration of a connection between the existing flora of the "Driftless Area," and that of the Lake Superior shore. This will be commented on again later.

A second species with a distribution pattern of a nearly similar type is *Diplophyllum obtusifolium* (Hook.) Dumort. (Fig. 13). The range of this species approaches that of *F. bolanderi* in several respects: the wide distribution along the Pacific Coast, where it is abundant (several stations not drawn in owing to lack of knowledge of the exact localities!), with a much more restricted range in the Great Lakes area (Minnesota, Michigan, Ontario). However, *D. obtusifolium* differs in its range in several respects from *F. bolanderi*. Unlike the latter, it is considered an oceanic species, Persson (1952) describing it as a "coastbound species;" it is also a more widespread species, not endemic to North America, ranging from western Europe to Iceland, and recently reported from Honshu, Japan (Amakawa and Hattori, 1955). More significantly, it occurs as a rare disjunct not only in the Great Lakes area, but also in the old Appalachian Region where it has recently been found.

The Minnesota, Michigan, Ontario, North Carolina and Tennessee material, i.e., the eastern population, differs in being predominantly or wholly autoecious and in the almost constant production of gemmae; in these respects it closely approaches *D. apiculatum*, to which the Minnesota plants were referred by Schuster (1953), as var. *obtusatum*. It seems certain now, however, that the var. *obtusatum* is much closer to D. *obtusifolium*. The Ontario material was kindly forwarded by Mr. H. Williams; it was collected at Cache Lake Outlet in Algonquin Park. The Tennessee plants were collected by the author on Myrtle Point, Mt. Leconte; the North Carolina plants were collected by the author in Linville Gorge, Burke Co.

The Appalachian populations of *D. obtusifolium* are unquestionably ancient. Equally ancient is the series of western populations, which extend in an arc from northern California to Attu I., in the Aleutians, southward to Honshu Island, Japan. The arc-like, oceanic western range of *D. obtusifolium* is strikingly similar to that of *F. bolanderi*, which extends from California northward to British Columbia, and then reappears on the island

of Sakhalin (Evans, 1915). As a consequence, the chief difference in the American range of *D. obtusifolium*, contrasted with that of *F. bolanderi*, lies in the retention of a disjunct Appalachian population in the former, vs. the evident lack of such a population in the latter. Also, the rarity of *D. obtusifolium* in the east makes it much more difficult to set up a plausible hypothesis as to the

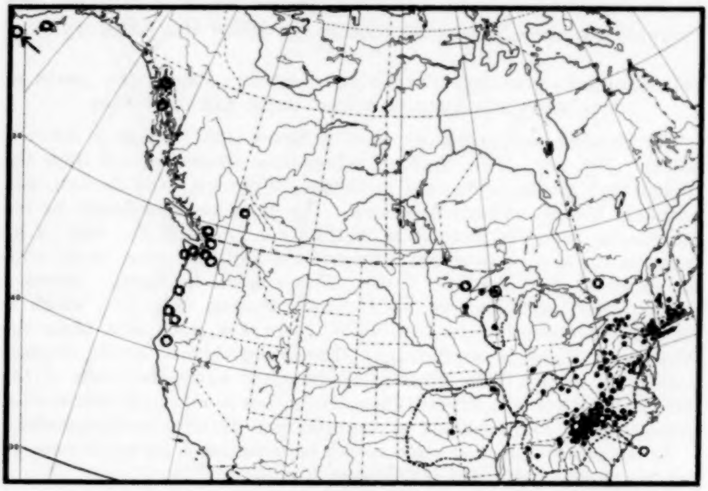

Fig. 13. Range of *Diplophyllum apiculatum* (dots) and North American range of *Diplophyllum obtusifolium* s. lat. (the eastern stations representing an undescribed subspecies). The Michigan station for *D. obtusifolium* was reported as *D. apiculatum* (Steere, 1947); it is based on plants collected at Bessemer (*M. S. Taylor, 1928*). Only two, juvenile, sterile plants have been seen with apiculate lobes; these, although hardly certainly determinable, could be referred to *D. apiculatum*. The single fertile plant, however, is not the same taxon; it bears a terminal perianth subtended by several cycles of sterile leaves; this perianth-bearing shoot bears innovations that are androecial (and, at least in one case, paroecious). In other words, the leading, gynoecial shoot bears male or bisexual innovations. This feature, together with the uniformly rounded ventral leaf lobes identifies these plants as the eastern race of *D. obtusifolium*

derivation of the Great Lakes population. The analogies in its range to that of *F. bolanderi* are at least suggestive.

If Fig. 12 and 13 are compared, a possible hypothesis for the origin of the easternmost stations of *Frullania bolanderi* can be derived by analogy to the existing range of *Diplophyllum obtusifolium*. Is it not possible that these eastern stations of *F. bolanderi*, the so-called "third center" of Steere (loc.cit.), were derived from an Appalachian refugium? Although *F. bolanderi*

is currently unknown from the northern end of the unglaciated Appalachian plateau, it would not prove at all surprising to find relict stations for it in this area.

The interpretation of the existing range of these two species must involve recognition of the fact that both are lowland species of forested areas, *D. obtusifolium* occurring only rarely (in Europe) in the higher mountains. Neither species can be interpreted as a "nunatak species," however loosely we define this category.

(4) CORDILLERAN SPECIES EXTENDING EASTWARD AND FOUND AGAIN IN THE DRIFTLESS AREA, BUT NOT ALONG LAKE SUPERIOR

The classical case, previously cited by Steere (1937) is that of *Asterella saccata* (Fig. 14). This thallose, calciphilous species, occurs from the Yukon and Alaska southward to Oregon, Wyoming, New Mexico, and probably Mexico, at high elevations. The plant has been found, by the Europeans, to be amphizonal in distribution, i.e., with the bulk of its range in the arctic-alpine, but a limited and scattered range as an xerothermophyte (see Reimers, 1940). This species, in Europe, shows a similar distribution pattern to *Athalamia hyalina* (Fig. 15), which is treated subsequently. In both cases, there is a small area along the Mississippi River, in southeastern Minnesota, where a totally disjunct population occurs. The physical environment along the bluffs of the Mississippi River is so different (basswood-maple forest on the rich wooded slopes) that it seems difficult to reconcile such distributional anomalies.

At the present time, no other species of *Hepaticae* is known to have an exactly parallel pattern of distribution.

(5) ARCTIC SPECIES OCCURRING IN THE DRIFTLESS AREA BUT NOT IN THE LAKE SUPERIOR REGION

During the period 1946–1950, the writer carefully investigated the high bluffs on the Minnesota side of the Mississippi River, facing Wisconsin to the east. On ledges on these bluffs, usually in rather dense shade, but occasionally near the exposed summits of the bluffs, were found two species with a wholly anomalous distribution. These occurred here, in part, in the shade of basswood-maple forest, on rich mesic slopes, associated with such "southern" species as *Reboulia hemisphaerica*. The existing range of these two species may have considerable bearing on the problem of the origin of the post-Pleistocene flora of the Great Lakes region.

Athalamia hyalina (Sommerf.) Hattori (Fig. 15). On a number of bluffs facing the Mississippi River, from Waccouta southward, i.e., at the edge of the "Driftless Area," small to extensive colonies of this arctic-alpine species were discovered. The plant is strongly calciphile. In North America, it appears to have a western, Cordilleran "center," from British Columbia and Alberta southward to California and Colorado, at

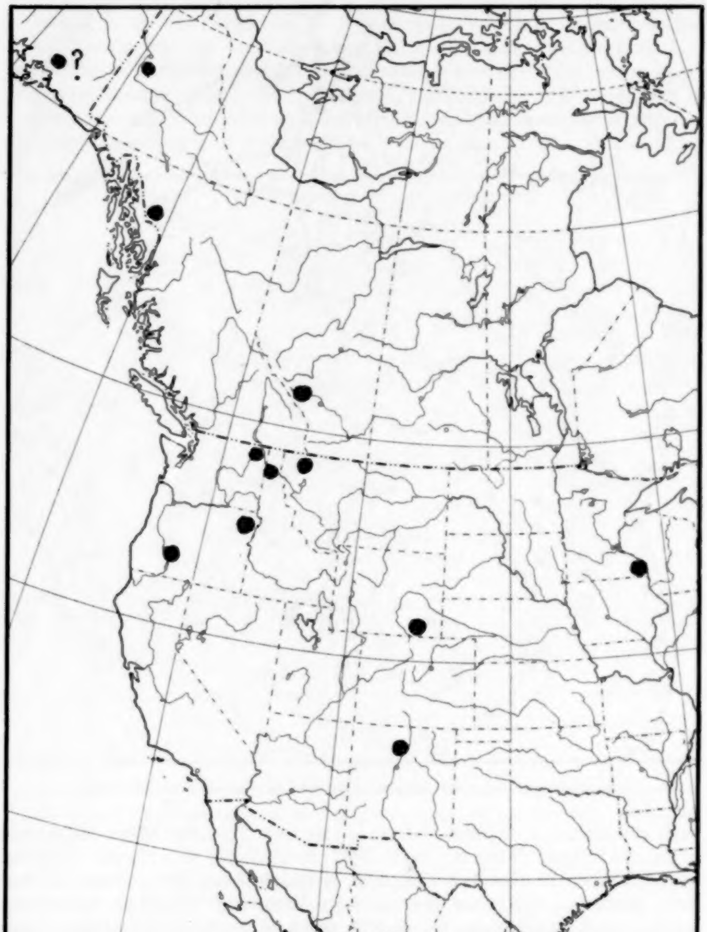

Fig. 14. North American range of *Asterella saccata*. The species is now evidently extinct at the Winona, Minn. station (see Schuster, 1953).

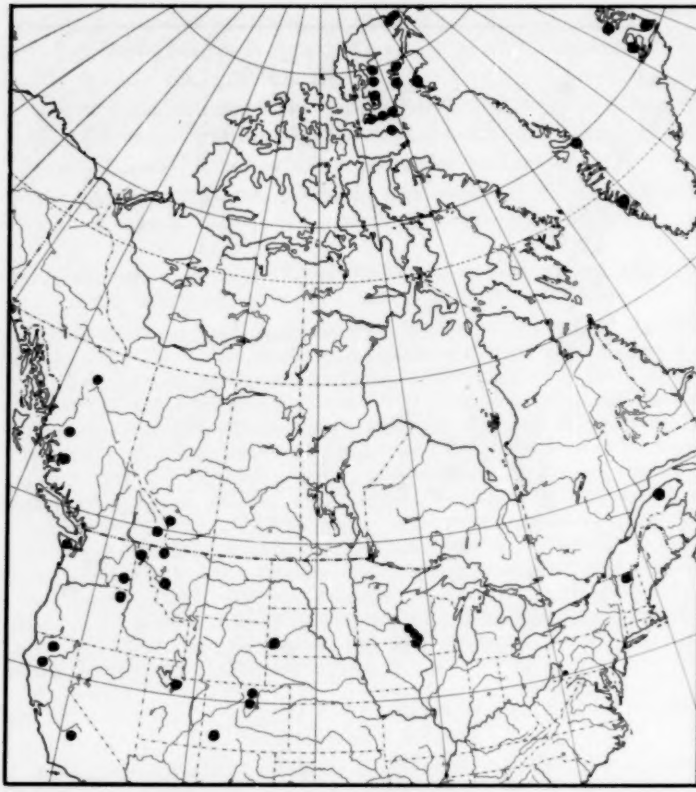

Fig. 15. North American range of *Athalamia hyalina* (= *Clevea hyalina*).

high elevations; a disjunct station is reported from the Black Hills area of South Dakota (Frye & Clark, 1937, in 1937–47; this report requiring verification). In the east, the plant is known from two collections, one from the Gaspé, the other from northern Vermont. However, the species appears to be much more frequent in the high Arctic, north of the Arctic Circle, on both coasts of Greenland, on Ellesmere Island to 82°32′ Lat. N., and south to Devon Island.[7]

[7] Perhaps a nearly parallel case is that of the essentially arctic-alpine *Sedum rosea* known from s.e. Minnesota in the form of a local race (var. *leedyi* Rosend. and Moore). *S. rosea* probably includes, *fide* Fernald (1950) "several so-called but scarcely separable species of w. N. Am." This ancient species, however, again occurs as a disjunct in the Appalachian region, from central New York to Roan Mt., North Carolina, but is widespread in the eastern North American Arctic, from Greenland to the coas of Maine. Except for the few Appalachian stations, at

The occasional occurrence of the species in Minnesota with *Mannia fragrans*, a xerothermophyte, at the summits of bluffs (bordering the "goat prairies" at the summit and on the western slopes of the bluffs), is suggestive of the isolated stations in Europe where the plant occurs as an xerothermophyte (Suza, 1938; Reimers, 1940; Müller, 1951–54). It is possibly more than coincidental that the only xerothermophyte occurrence of *Asterella saccata* in North America is in the same area. It should be

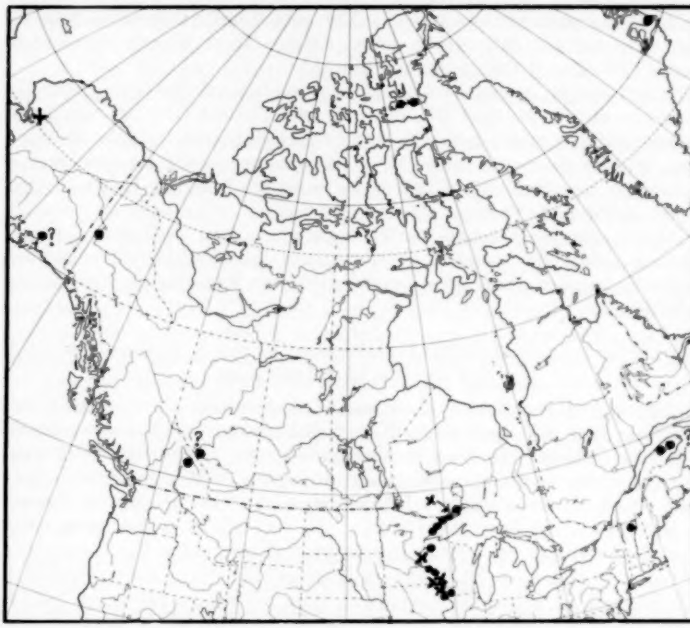

Fig. 16. North American range of *Mannia pilosa* (dots) and the doubtfully distinct *M. sibirica* (crosses).

noted that the European students who have carefully investigated the occurrence of these two arctic-alpine species, also often occurring with the "southern" xerothermophytic *Mannia fragrans* in Europe, have concluded that these represent cases of physiological adaptation by Pleistocene relicts. The restriction of the two species to the "Driftless Area" thus acquires special significance.

which the plant is a clear relict. *S. rosea* (L.) Scop., *sensu lato*, has a distribution pattern very closely paralleling that of the *Athalamia*, although not penetrating to as nearly as high a latitude as the latter.

Particularly striking, in this case, is also the connection established between the Driftless Area, and the Appalachian Region (in both of which the *Sedum* occurs as a relict!).

Mannia sibirica (K. Müll.) Frye and Clark. (Fig. 16, crosses). This species is reputed to be a high arctic type, although it has been collected so few times that any conclusion must be regarded as tentative. Virtually all of the few collections, from Norway and Siberia, are from the far north. The only previous report is of a single collection from Alaska (Clark & Frye, 1942). During the years 1947–1950 the writer found this species, in typical manifestations, a number of times at the edge of the "Driftless Area," and slightly to its north, in the St. Croix R. valley, i.e. in the same area as *Athalamia hyalina*, and usually associated with it. For exact locality data see Schuster (1953). These reports represent a major extension of the species southward.[8]

Unfortunately, as has been previously emphasized (Schuster, 1953), it is still uncertain whether *M. sibirica* is fully distinct from *M. pilosa* the latter having a wider but still arctic-alpine distribution (dots on map, Fig. 16). If the ranges of the *M. sibirica-pilosa* complex are combined, a nearly continuous series of collections is shown from the Driftless Area north to the Lake Superior shoreline (Fig. 16).

I have also seen several sterile fragments, mixed with spores, representing either this species, or the almost inseparable (when sterile) *Asterella ludwigii*; these plants were collected in lime sinks in Alpena Co., Michigan.

(6) Arctic species occurring southward to the Lake Superior area and in the Driftless area

Although a number of *Hepaticae* of northern affinity occur in the Driftless Area, and again on the Lake Superior shore (*Scapania mucronata, Preissia quadrata, Tritomaria exsectiformis*, etc.), only two taxa with an essentially arctic-alpine distribution occur in both the Driftless Area and along the cold shores of Lake Superior. One species is *Mannia pilosa* (Hornem.) Frye and Clark, s. str. As will be noted below, it is not clear whether *M. sibirica* can be kept distinct from this. In either eventuality, the same basic pattern remains (Fig. 16). *Mannia pilosa* is known from a station in Greenland, from several in Ellesmere Island, and from the Alaska-Yukon region; it occurs south of the Arctic Circle only in the high Cordilleras along the Alberta-British Columbia boundary, in the Gaspé Mountains, and at a single station on Willoughby Mt. in Vermont. It then recurs, locally and usually in only small quantity, in western Wisconsin, and in eastern Minnesota and northeastern Iowa. The latter portion of its range extends from the Driftless Region northward to the north shore of Lake Superior. This distribution pattern, in some ways, serves to unite patterns 1 and 5 into a single unit. The implications of this are discussed in the final summation.

[8] Dr. H. Crum of the Canadian National Museum has just submitted a specimen of this species to me for verification. This was collected at Ft. William, Ontario, near the Lake Superior shore (May, 1955).

(To be concluded)

SOME NEW FLORAS FOR PARTS OF NORTH AMERICA.—Although the total number of species of higher plants in the high arctic is not great, comparatively, the importance and complexity of the plant cover in connection with geomorphic processes is being increasingly recognized. This means that an ever larger number of investigators outside of botany concerned with research on arctic lands are becoming interested in the kinds of plants growing there. The excellent recently published ILLUSTRATED FLORA OF THE CANADIAN ARCHIPELAGO[1] by A. E. Porsild provides a sound coverage of the flora for most purposes. This work, with neat realistic drawings of each species by Mrs. Dagny Tande Lid, provides keys to the families, genera and species, brief descriptions and notes concerning each species and a map showing the total range in northern Canada.

Another book of outstanding quality concerned with the Canadian flora is: FLORA OF MANITOBA[2] by H. J. Scoggan. Here is a volume that ranks with the best state and provincial floras and is superior to most of them. The work covers all species and well marked varieties, native or introduced, known to occur within the provincial boundaries. There are keys to the families, genera, species and varieties and notes concerning the habitat and geographical distribution of each species or variety. Descriptions are omitted. The first 37 pages are devoted to the history and scope of the flora together with a discussion of the physical features of Manitoba, its climate and vegetation and the affinities of the flora. Scoggan has critically dealt with literature and specimen records for the Province, excluding many names shown to have been incorrectly applied or otherwise not authenticated as part of the present-day flora. In an analysis of Manitoba's flora, Scoggan finds 1,417 species and 124 subspecies or varieties of vascular plants present. This contrasts with 340 species, subspecies or varieties reported by Porsild for the Canadian Archipelago.

SPRING FLORA OF THE DALLAS-FORT WORTH AREA, TEXAS[3], by Lloyd H. Shinners, covers the ten counties immediately surrounding these two cities, but the book will have application to a considerably wider area. Plants blooming between January 1st and the first week of June are particularly included in the work, but many early summer blooming types are also mentioned. There are keys to the families, genera and species, and notes on outstanding characteristics, habitats, geographical distribution and blooming dates. Much of the originality in the book is found in the appendices where one finds a discussion of technical terms, the use of keys, scientific and common names, pronunciation, rules of nomenclature, collecting herbarium specimens, natural history of plants, conservation and notes on the background of the book. This book is definitely student

[1] National Museum of Canada, Bulletin No. 146. pp. 1–209. 1957. Paperbound $2.00.

[2] National Museum of Canada, Bulletin No. 140. pp. 1–619. 1957. Buckram $5.00.

[3] Spring Flora of the Dallas-Forth Worth Area, Texas by Lloyd H. Shinners. 514 pp. 1958. Paperbound $5.50 ($5.75 by mail). Published by the author and available at S.M.U., Box 473, Dallas 5, Texas.

oriented. It is produced by photo-offset printing and the paper covers and pages are held together by a plastic spring binding.

This book, though both seasonally and geographically limited, is of considerable importance because it pertains to an area that has not been adequately covered by a flora.

SPRING FLORA OF CENTRAL OKLAHOMA[4] by George J. Goodman is similar in many ways to Shinner's book. It is produced by photo-offset printing, has a large page size and the flexible paper cover, together with the pages, are held by a plastic spring binding. The book has keys to the families, genera and species which bloom before June 1st in the central area of Oklahoma and is obviously designed for use by students at the University of Oklahoma. Nevertheless, it is a valuable addition to the floras covering portions of the United States. There are short notes on habitats and geographic ranges under each listed species. As pointed out by Dr. Goodman, the area covered is almost entirely in the Permian Red Beds and possesses a rich and varied flora. Some 716 species and infraspecific taxa are included in the work.—R. C. Rollins, GRAY HERBARIUM, HARVARD.

[4] Spring Flora of Central Oklahoma by George J. Goodman. Published by the University of Oklahoma Duplicating Service, Norman, Oklahoma. 1958. 12[illegible] pp. Paperbound $3.35.

Volume 60, No. 715, including pages 177–208, was issued 6 August, 1958.

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These books have library book plates and are used copies, some worn, some in need of binding.

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